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Natural History and Ecology of Fowler's Toad, *Bufo woodhousei fowleri* (Amphibia: Bufonidae), in the Indiana Dunes National Lakeshore

Felix Breden

A Contribution in Celebration
of the Distinguished Scholarship of Robert F. Inger
on the Occasion of His Sixty-Fifth Birthday

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- LANGDON, E. J. M. 1979. Yagé among the Siona: Cultural patterns in visions, pp. 63-80. In Browman, D. L., and R. A. Schwarz, eds., *Spirits, Shamans, and Stars*. Mouton Publishers, The Hague, Netherlands.
- MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, *The Andean Civilizations*. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
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Natural History and Ecology of Fowler's Toad, *Bufo woodhousei fowleri* (Amphibia: Bufonidae), in the Indiana Dunes National Lakeshore

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Natural History and Ecology of Fowler's Toad, *Bufo woodhousei fowleri* (Amphibia: Bufonidae), in the Indiana Dunes National Lakeshore

Abstract

A four-year mark-and-recapture study of a population of Fowler's toad was conducted in the West Beach Unit of the Indiana Dunes National Lakeshore. This study estimated the demographic characteristics and potential for dispersal among breeding areas in this species. Population size was estimated as 1,814 adults, with only 150 egg masses laid in spring 1981 producing free-swimming larvae. Relatively more dispersal from the natal areas occurred at the prereproductive, juvenile stage than during the older age classes, although dispersal was observed at all life history stages. While a strong male-biased sex ratio was observed in the breeding aggregations, the actual population sex ratio was not biased toward either sex. Females grew more quickly and attained a larger adult size than males, but became sexually mature at the same age, two years after metamorphosis. The life table calculated for this population showed a type III survivorship curve, with less than 0.1% of all eggs surviving to the age of first reproduction. Given the restriction of breeding areas of this species by specific habitat requirements and the intense utilization of the dunes area by humans, local extinctions of this species could be expected to be permanent events.

Introduction

Fowler's toad, *Bufo woodhousei fowleri*, is a common toad of the eastern United States, occurring in a variety of seasonally wet habitats, including riverbanks, flooded fields, and ponds (Conant, 1975). However, in the northern part of

its range, this species has very specific habitat requirements and is found only in areas characterized by open vegetation and sandy substrate. Hence, in northern Indiana and Michigan, Fowler's toads occur primarily on the early successional, open sand dunes found close to the southern and eastern shores of Lake Michigan. This restricted habitat has been fragmented by intense industrial and residential development, and therefore many of the populations of Fowler's toad in this region occur as "insular" populations whose fate may be precarious. Little information is available on the dynamics of such populations. In this paper I report on the ecology and natural history of one restricted population of Fowler's toad found in the Indiana Dunes National Lakeshore.

Several general patterns of the natural history of amphibians have important implications for the ecology and evolution of local populations. First, many species breed in aquatic sites that occur in patchy distributions. This geographical structure is reinforced by the precise homing behavior exhibited by many species, in which breeding adults return to the same areas each year (e.g., *Ascaphus truei*, Daugherty & Sheldon, 1982; *Bufo* spp., Awbrey, 1963; McMillan, 1963; Oldham, 1966; Ewert, 1969; Heusser, 1969; Tracy & Dole, 1969a,b; Grubb, 1973; *Taricha* spp., Twitty, 1961, 1966; *Notophthalmus viridescens*, Gill, 1978). It has been suggested that adult homing behavior to restricted breeding sites could result in genetic differentiation among amphibian breeding aggregations, owing to reduced migration (Tabachnick & Underhill, 1972; Christein et al., 1978; Hedgecock, 1978; Howard & Wallace, 1981; Daugherty & Sheldon, 1982). Such restriction of gene flow, coupled with the highly specific habitat requirements of Fowler's toad and destruction of this habitat in the

Indiana Dunes region, could lead to an increase in the level of homozygosity in these areas and create conditions favorable to local extinctions. It is interesting to note that a disjunct population of Fowler's toad, previously occurring north of Chicago, has been eliminated since the early 1900s. This population was associated with the small dune system found in Lake County, Illinois, along the northern shore of Lake Michigan. Following industrialization and residential development in this region, this habitat has been restricted to a small portion of Illinois Beach State Park.

The tenuous conditions of restricted populations of amphibians demand detailed demographic and dispersal studies. Ideally the demographic data would indicate probabilities of extinction and minimum viable population sizes, and the data on dispersal would indicate the potential for recolonization of areas from which species have disappeared. Such studies can then be used to evaluate the effects of loss and isolation of habitat on these species. However, there are few studies of amphibians that combine estimates of survivorship schedules, growth rates, population sizes, and other demographic characteristics with data on dispersal at all stages of the life cycle. Although many studies of adult amphibians are available, few studies have been able to investigate these parameters beginning with larval and metamorphic stages (see Breden, 1982, 1987). This is partly due to the fact that larval and newly metamorphosed individuals are small and difficult to mark. This paper presents a description of the amount of dispersal occurring at all life history stages and the age-specific demographic characteristics of Fowler's toad.

Another aspect of amphibian natural history that might have important evolutionary and ecological consequences is the male-biased sex ratio observed at breeding areas. This has often been reported in the genus *Bufo* (e.g., Oldham, 1966; Heusser, 1969; Christein & Taylor, 1978; and Gittins et al., 1980). Such a skewed sex ratio could strongly influence the force of sexual selection by increasing the variance in reproductive success among males (Wade & Arnold, 1980) and thereby decreasing effective population size (Crow & Kimura, 1970). A male-biased sex ratio could be caused by at least three factors, each working separately or reinforcing one another: (1) males might stay in breeding aggregations for the entire season, while females remain for only a short period of time; (2) males might reach reproductive maturity

at an earlier age than females; and (3) females might not breed each year. Because females usually are larger than males at reproduction and if females and males mature at the same age, then females must grow at a faster rate than males. For the third factor to be important, a significant proportion of the population would have to survive several years past the age of first reproduction. Obviously, an understanding of the causes of a skewed sex ratio requires data from animals of known ages. In this study, data on age at sexual maturity, sex-specific growth rates, and actual sex ratio in the population are used to examine the causes of the observed sex ratio at Fowler's toad breeding sites.

Materials and Methods

Study Population and Habitat

Fowler's toads are common in the Indiana Dunes region and are a characteristic species of the open, sparsely vegetated dunes that occur near the shore of Lake Michigan. This type of habitat is abundant in the main study site, the West Beach Unit of the Indiana Dunes National Lakeshore, Porter County, Indiana. The herpetological collection of Field Museum of Natural History has animals collected from this locality dating from 1902. The main study site is 250 ha; of these, approximately 150 ha are open, sandy dunes and sparse grasslands interspersed with "blowouts" (areas where natural vegetation has been disturbed and wind erosion has removed large amounts of sand) and interdunal ponds. The area is bounded on the north by Lake Michigan and on the south by Long Lake, a shallow, large interdunal lake (fig. 1). South of Long Lake the habitat consists of more heavily vegetated, older dunes which are not suitable for Fowler's toads. The west and east boundaries are formed by heavily populated areas, and habitat suitable for Fowler's toads has been destroyed. Therefore, the area is isolated from other populations, the nearest of which is approximately 7 km southwest. The area was not developed (except for some sand-mining not in the area of the ponds) because it was owned by a steel company until it became part of the Indiana Dunes National Lakeshore in 1966.

The dominant topographic features of the study site are the parallel ridges of dunes extending

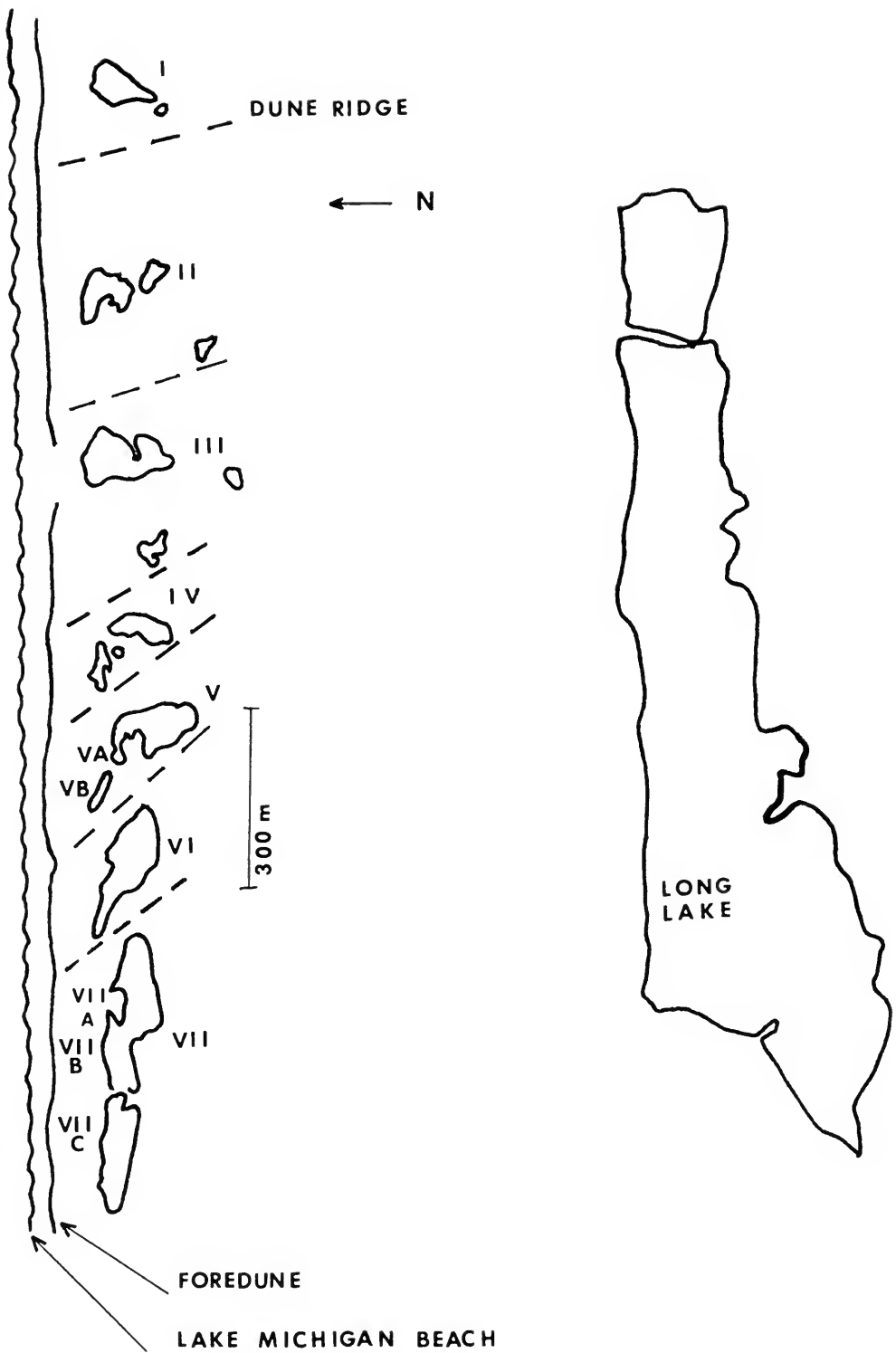


FIG. 1. Schematic drawing of main study site in the West Beach Unit of the Indiana Dunes National Lakeshore, showing seven divisions, labeled I–VII, separated by high dune ridges (dashed lines).

southeast from the foredunes (20 m south of the lakeshore) to the large dunes in the southern part of the park (approximately 350 m south of the lakeshore). These ridges, indicated in Figure 1 by dashed lines, extend from 50 to 100 m above the level of the lake and define a linear array of seven depressions, stretching 2 km along the beach. Each of these areas contains several shallow, sand-bottomed ponds, in which Fowler's toads breed. These seven sets of ponds, separated by high dune ridges, provide the geographical structure within which the pattern of toad movement was measured. Migration is defined as movement among these seven areas, which are numbered sequentially (I–VII) from east to west (see fig. 1). These ponds probably have been predictable breeding sites for this species for at least several decades.

Aerial photos from 1938, 1958, and 1973, produced by the United States Department of Agriculture and on file at the Indiana Dunes National Lakeshore, show that the position of the main ponds and the overall topography of the West Beach Unit have remained constant for at least the past 50 years. This is perhaps surprising, given the "shifting" nature of the dune habitat. However, these large dune formations apparently do not change position very quickly; therefore, ponds associated with them are predictable breeding sites. All of the areas retained water and produced metamorphic toadlets throughout the summers of 1977–1983. This consistent presence of water may reflect the fact that Lake Michigan's water level has been relatively high for these years (Meyer & Tucci, 1979).

The ponds in these seven areas are physically very similar and are associated with the same animals and plants. They are shallow (up to 1.5 m deep), with sandy bottoms and gradually sloping banks. During dry periods in summer and fall the ponds shrink, and often only the deepest sections retain water. There are a few patches of cattails (*Typha* spp.) and algal mats (*Chara* and other spp.); the vegetation in the ponds consists primarily of sedges (*Carex* spp.) and bulrushes (*Scirpus* spp.). Common plants surrounding the shores of the ponds are sedges, bulrushes, bog arrow grass (*Triglochin maritima*), rush plants (*Juncus* spp.), and Kalm's St. John's wort (*Hypericum kalmianum*). The open dunes surrounding the ponds are dominated by sand cherry (*Prunus pumila*), marram grass (*Ammophila brevigulata*), cottonwood (*Populus deltoides*), sand thistle (*Cirsium pitcheri*), and little bluestem (*Andropogon scoparius*). The ponds in the two outermost areas (I and VII) are some-

what deeper and more vegetated, dominated by cattails and algal mats. A few *Bufo americanus* bred in areas I and VII during the years 1977–1981. Fowler's toads breeding in areas I and VII consistently bred only in the smaller ponds and in the regions of the larger ponds that were similar to those in the interior of the park.

Mark and Recapture

Fowler's toads breed in the interdunal ponds in the spring, tadpoles metamorphose in June and July, and many juveniles and adults spend summer and fall on the foredune and beach of Lake Michigan (Stille, 1952). I marked animals and monitored movements at several stages of this life cycle. Tadpoles that had an electromorph unique to the study area were introduced into one pond, metamorphic individuals from several areas were marked with a system that identified only the area from which they emerged, and juvenile and adult toads were individually marked. In the next two sections, I briefly describe the physical and electrophoretic marking techniques used (for full details see Breden, 1982).

PHYSICAL MARKING—The identification system for adults combined the removal of a total of two toes, one from a front foot and one from a hind foot, with freezing a brand into the dorsal skin using copper wires frozen in liquid nitrogen. In a few instances where these marks were not clear, numbered Floy fish tags were secured in the skin by loops of nylon monofilament wire. Of the 2,445 mark-and-recapture events involving individually marked toads, 1,260 animals were captured once, 251 twice, 109 three times, 49 four times, 22 five times, 6 six times, and 2 seven times.

Metamorphic toadlets were given an area-specific mark by removing the two outermost toes from one foot. This system produced four possible identifications, and animals from areas I, III, IV, and VII were marked. A total of 6,079 metamorphic toadlets were marked during 1979, and 2,460 during 1980. There was some regeneration of toes, identifiable by a whitish color, but never well-formed toes. Many of these animals were recaptured as juveniles and were then individually marked.

ELECTROPHORETIC MARKING—In order to introduce individuals genetically marked with a unique electromorph, an electrophoretic survey (Selander et al., 1971) was conducted of the West Beach Unit and other populations from Indiana, Michigan,

Illinois, and Arkansas. From this survey, a glutamate oxaloacetate transaminase (GOT) electromorph (table 1) was chosen for the introductions. Males homozygous for this marker were identified by electrophoresis of their toes and mated in the laboratory to females from the study population or from other dune areas. This produced offspring known to carry the unique allele. These crosses showed that this electromorph was inherited according to mendelian ratios. When these marked tadpoles were one week old, more than 17,000 were introduced into one pond in area V (fig. 1). Toes removed from adults as part of the individual marking system were saved in the field on wet ice, stored in the laboratory at -40°C , and examined by electrophoresis. This provided a method of examining adult toads, without killing them, for the presence of the unique electromorph that had been introduced at the larval stage, and for determining levels of heterozygosity in this population.

Each pond was visited approximately every other night during the 1977–1981 breeding season. Positions of toads were marked according to the pond of capture. During the summers of these years, the area of the shore and foredune of Lake Michigan (fig. 1) was searched for toads and the exact position along the beach was determined for each capture. The length of the body from snout to vent or the length of the astragalus-calcaneus complex was measured on each animal. The length of the astragalus-calcaneus complex did not change with pressure exerted on the animal; it was therefore a highly repeatable measure and was used most often. To present the results in terms of a standard measure, all measurements were transformed to snout-vent lengths by the equation:

$$3.19 + (1.8 \times \text{astragalus-calcaneus complex length})$$

This equation was determined by measuring both lengths on 147 toads. The regression equation from these data explained 89.3% of the observed variance ($P < 0.0001$).

Estimating Number of Adults per Breeding Aggregation

Two methods were used to estimate the size of the breeding population in each of the seven areas. First, all of the mark-and-recapture records from spring 1981 were divided into two samples: an initial marking period and a second recapture period. These data were then analyzed by a Lincoln-

TABLE 1. Allozyme variation at three polymorphic loci in Indiana, Michigan, Illinois, and Arkansas populations of Fowler's toad, *Bufo woodhousei fowleri*.

Locus	Alleles	Locality frequencies (sample size in no. of genomes)			
		Indiana Dunes*	Michigan Dunes†	Illinois‡	Arkansas§
GOT	M	1.00	0.98	0.83	0.75
	F	0.00 (136)	0.02 (92)	0.17 (18)	0.25 (44)
PGM-II	M	1.00	1.00	0.57	1.00
	F	0.00 (192)	0.00 (98)	0.43 (14)	0.00 (42)
GAPDH	S	0.00	0.08
	M	1.00	0.83
	F	0.00 (98)	0.08 (12)

* Porter Co., Ind.

† Mason and Muskegon Cos., Mich.

‡ Mason Co., Ill.

§ Lawrence Co., Ark.

Petersen model for a geographically stratified population (Overton, 1971). Because I was not able to catch many females in the spring, this estimate was based only on male recaptures. A second determination of the number of adults breeding in each area was made by counting egg masses. I visited each pond at least twice per week during spring 1981. On these visits egg masses were mapped, counted, and the number of masses producing free-swimming larvae was noted. Although toads lay eggs in long strings, females tend to reverse their paths during oviposition and intertwine egg masses within small clumps of vegetation. These discrete masses of dark eggs were easily detected against the sandy bottoms of the shallow ponds. Because the deeper areas of some ponds had more humus and were harder to survey, especially in areas I and VII, some egg masses probably were missed. Therefore, this second estimate of the number of reproducing adults will be treated as a lower bound.

Results

Electrophoretic Variation of Fowler's Toad Populations

Although the main purpose of the electrophoretic survey was to discover alleles not present in

the study site that could be used as markers, the population allele frequencies show a relatively high degree of homozygosity in the study site. Of 23 loci, only one locus was polymorphic in both the West Beach Unit and other populations. Of the remaining 22 loci, eight were polymorphic in the other study sites but monomorphic in West Beach. This analysis did not include esterases and general proteins, because their genetic interpretation was not confirmed by laboratory crosses. Table 1 shows the allele frequencies for GOT, glyceraldehyde phosphate dehydrogenase (GAPDH), and a phosphoglucumutase (PGM-II) system, the three most thoroughly analyzed loci. Even though a much larger number of animals was tested from the main study site than from any other population, no variation was discovered in the West Beach Unit, while some variants were found in other populations.

Seasonal Activity Pattern

The seasonal activity pattern of Fowler's toads was consistent for the four years of this study. The earliest dates for male chorusing for the years 1978–1981 were 11 May, 10 May, 6 May, and 4 May, respectively. The lowest evening air temperature recorded for a night on which males chorused was 10°C, although large choruses occurred only at temperatures of 16°C or higher. These dates of earliest activity and minimum temperature requirements for breeding activity correspond well with those reported for Fowler's toads near South Bend, Indiana (Cory & Manion, 1955), although the temperature minimum is lower for West Beach.

The appearance of egg masses was used as an indication of the initiation of female breeding activity. During the 1981 breeding season, during which all ponds were surveyed for egg masses, the earliest egg mass was deposited on 4 May and the latest on 7 June. For all four years, the latest egg mass was laid approximately 24 June (1980). As in many anuran species, males often chorused for several weeks after the last egg mass was deposited. The earliest date for metamorphosis was 3 July, the latest 18 July. Thus metamorphosis occurred during a two-week period for all of these years, although the deposition of egg masses occurred during a period more than twice as long. Competition among tadpoles might contribute to this decrease in the range of metamorphosis times compared to egg deposition times (see Breden & Kelly, 1982).

After the breeding season, many females and

males moved to the shore of Lake Michigan, the beach "summer quarters." Many toads returned to the same summer quarters for several years in a row (Breden, 1982). Similar movement patterns were observed in the Indiana Dunes by Shelford (1913), Hubbs (1918), and Stille (1952). The earliest record of this beach-frequenting behavior was during the first week of May (1979). Females generally moved to the beach before males. In all years both males and females were captured in their summer quarters by late June, even though there were still active choruses at the breeding ponds.

During late August, animals that metamorphosed the preceding summer reach a snout-vent length greater than 30 mm, designated as "juveniles" in this study. At this time a large proportion of the juveniles leave the moist vicinity of the ponds and migrate to the beach. This movement pattern is reflected in the proportion of beach captures that were juveniles for nights when at least five animals were captured. This proportion for 1978 and 1979 was 0% from early July until mid-August, at which time it increased to almost 100%. In 1980 the proportion of juveniles ranged from 10% to 50% from July to early August, and then increased to nearly 90% by late August. During September few adults were captured on the beach, but juveniles remained active until late September.

Age-Specific Dispersal Patterns

DISPERSAL OF ANIMALS MARKED AT METAMORPHOSIS—The amount of dispersal from the natal areas for all life history stages can be estimated from records of animals given an area-specific mark at metamorphosis. Figure 2 shows the distribution of dispersal distances, measured in number of areas moved from the natal area, for animals marked at metamorphosis and recaptured as juveniles (first fall postmetamorphosis, $N = 29$), as subadults (first spring postmetamorphosis, $N = 37$), and as breeding adults (two years postmetamorphosis, $N = 37$). Animals marked at metamorphosis and recaptured as adults in breeding aggregations provide the best data on the potential for successful dispersal. Of 37 such animals, 27 were recaptured in the natal area, 5 had moved one area away, 4 two areas away, and 1 six areas away (a distance of approximately 2 km); 30 had been physically marked at metamorphosis, and 7 had been electrophoretically marked as tadpoles. The distributions of dispersal distances for the three life his-

tory stages were not significantly different between electrophoretically and physically marked animals ($P > 0.5$ for all chi-square contingency tests, pooling distances 3–6 or 2–6). Therefore, all subsequent analyses of dispersal postmetamorphosis combine data from these two marking techniques.

A comparison of the dispersal distribution from metamorphosis to the juvenile stage with that from metamorphosis to adult stage (fig. 2A,C) shows that a larger proportion of animals was observed away from the natal pond at the earlier life history stage. The proportion recaptured in natal areas as juveniles (15 of 29) was significantly lower than the proportion recaptured as adults (27 of 37) ($0.05 > P > 0.01$, Fisher's exact test). If animals tended to disperse during the juvenile stage, and continued to disperse at the same rate as adults, then the proportion of animals recaptured at their natal ponds would be expected to decrease with age. However, the opposite trend was observed.

AGE-SPECIFIC MOVEMENT PROBABILITIES—The above results from animals marked at metamorphosis suggest that most dispersal occurs during the first year. Additional information on age-specific dispersal can be obtained from the large number of observations of animals marked for the first time as juveniles and subadults. In Table 2, two measures of movement have been estimated from these data: (1) the proportion of animals moving during each life history stage, captured anywhere in the study site; and (2) the median linear distance dispersed between captures on the Lake Michigan beach, where positions were known to an accuracy of 10 m. For the second analysis, the point of origin for metamorphic animals was estimated as the point on the beach closest to the center of the pond of metamorphosis. The data in Table 2 show that almost 50% of the animals recaptured as juveniles dispersed away from their natal ponds, but only 12%–17% of the animals captured at later life history stages had moved from their previous capture sites. Furthermore, the median linear distance moved from metamorphosis to the juvenile stage was 174 m, whereas the median distances moved during later stages were all less than 29 m. The conclusion drawn from this analysis coincides with that based solely on the movement of animals marked at metamorphosis: many animals disperse from their natal ponds during the first year, but fewer disperse during the later ages.

ESTIMATION OF PER-GENERATION MIGRATION RATE—Three types of information were used to calculate the amount of migration (and hence gene flow) among breeding aggregations per generation:

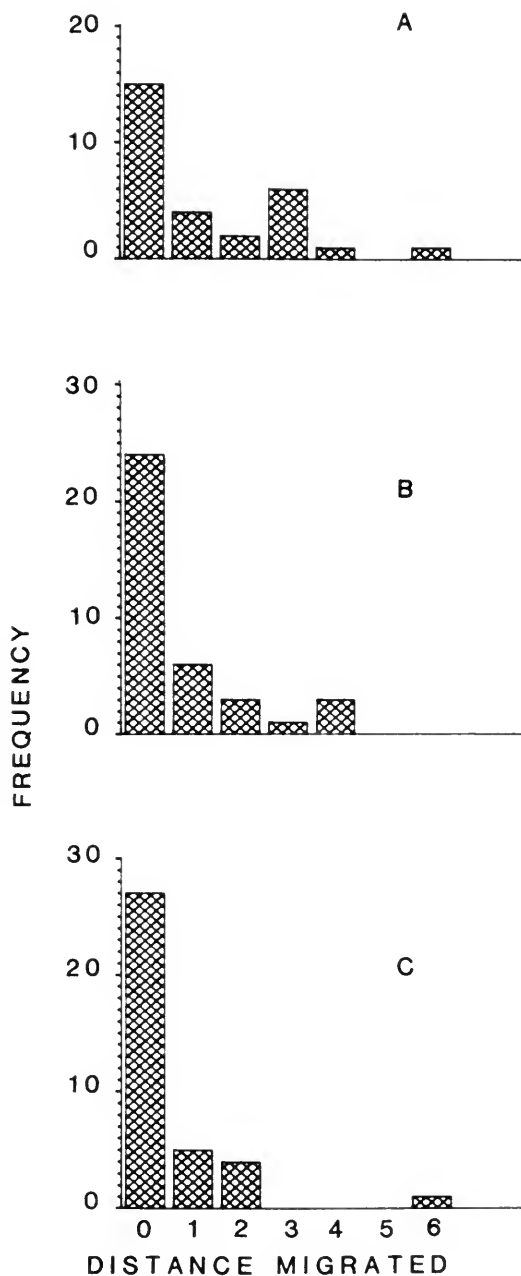


FIG. 2. Distance migrated from the natal area: A, juveniles (first fall postmetamorphosis); B, subadults (second year postmetamorphosis); and C, adults (two years postmetamorphosis). Distance is measured in units of the geographical subdivisions of the study site, each area consisting of several ponds separated by high dune ridges.

TABLE 2. Proportion dispersing and linear distance moved for each life history stage.

Life history stage*	Proportion dispersing between captures	Median distance dispersed between beach captures
Metamorphosis to juvenile	$\frac{14}{29} = 0.48$	174 m (N = 14)
Juvenile to subadult	$\frac{4}{34} = 0.12$	25 m (N = 16)
Subadult to adult	$\frac{4}{26} = 0.15$	25 m (N = 7)
Adult, year t to year t + 1	$\frac{24}{140} = 0.17$	29 m (N = 28)

* Juveniles, 2–3 months postmetamorphosis; subadults, 10–14 months postmetamorphosis; adults, more than 2 years postmetamorphosis.

(1) distribution of dispersal distances observed from metamorphosis to the age of first reproduction; (2) probability of further dispersal during any adult year; and (3) turnover rate of the adult population. When these factors are taken into consideration, I estimate that 49% of a cohort’s expected breeding takes place in areas other than the natal area (for details of this calculation see Breden, 1987).

Postmetamorphic Growth Rate and Age at Sexual Maturity

A large number of animals of known age were followed through postmetamorphic development to determine age-specific growth rates. Table 3

lists the mean body length and change in mean body length for six age classes.

Toads metamorphosing in July at a very small size (average 9.0 mm) grow to an average of 46.8 mm by September of their first fall postmetamorphosis. From fall to the next spring very little growth occurs. From the first spring to the second fall, animals complete most of the remaining post-metamorphic growth and reach an average length of 59.7 mm. Although the change in mean body length during the second growing season is only 9.7 mm, this represents a large increase in body volume. As an illustration, for two preserved specimens there was a 341% increase in body volume from 8.5 ml (snout-vent 48.4 mm) to 37.5 ml (snout-vent 60.0 mm), corresponding to the growth expected during this second growing season post-metamorphosis. This average size attained by the end of the second fall after metamorphosis equals the size at which animals reach sexual maturity. Mean size at sexual maturity was estimated as 59.2 mm from animals captured as two-year-olds (known from marks at metamorphosis) and in breeding condition (ascertained in males by secondary sexual characters and in females by being in amplexus). Thus, by the second fall postmetamorphosis, animals have attained the size of sexual maturity, but they cannot breed until the following spring.

This schedule of postmetamorphic growth is reflected in the distributions of snout-vent lengths in the spring and fall capture records. Figure 3A presents the snout-vent lengths of all animals captured during the fall of any of the four field seasons, and shows two distinct size classes. One is centered at 46.3 mm and presumably consists of animals that metamorphosed the previous July. The second distribution is centered at 58.9 mm, and is

TABLE 3. Postmetamorphic growth rates (snout-vent length in mm).

Stage	Month	Age (mo)	Mean (SE)	Change from previous stage
Metamorphosis	July	0	9.0 (0.2) (N = 60)	...
Juveniles (first fall)	September	2	46.8 (0.2) (N = 281)	37.8
Subadults (first spring)	May–June	11–12	50.0 (0.3) (N = 41)	3.2
Subadults (second fall)	September	14	59.7 (0.5) (N = 44)	9.7
Adults (second spring)	May–June	23–24	59.2 (0.3) (N = 68)	–0.5
Adults (third spring)	May–June	35	61.1 (1.6) (N = 5)	1.9

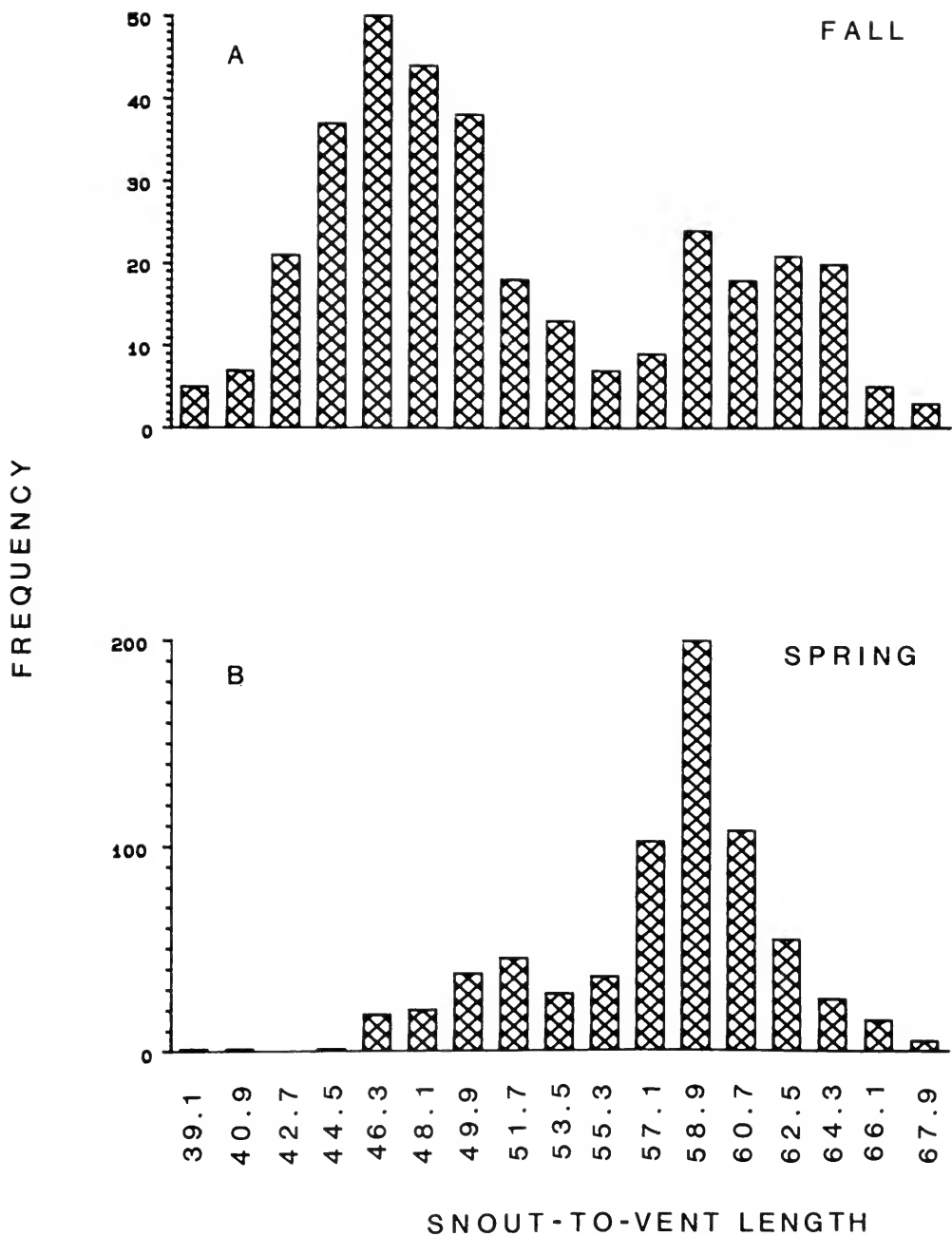


FIG. 3. Distribution of snout-to-vent lengths: A, fall (N = 348); and B, spring (N = 696) captures.

composed of adult animals. Figure 3B presents the snout-vent lengths of all animals captured during the spring of any of the four field seasons and shows two peaks, one at 51.7 mm and one between 58.9 and 60.7 mm. Comparing these two distributions, it is apparent that from one fall to the

next spring the mean of the juveniles shifts from 46.3 to 51.7 mm, while the distribution of adult sizes remains centered near 58.9 mm. This analysis reinforces the conclusion that size at maturity is approximately 59 mm, and that little growth occurs after this size is attained.

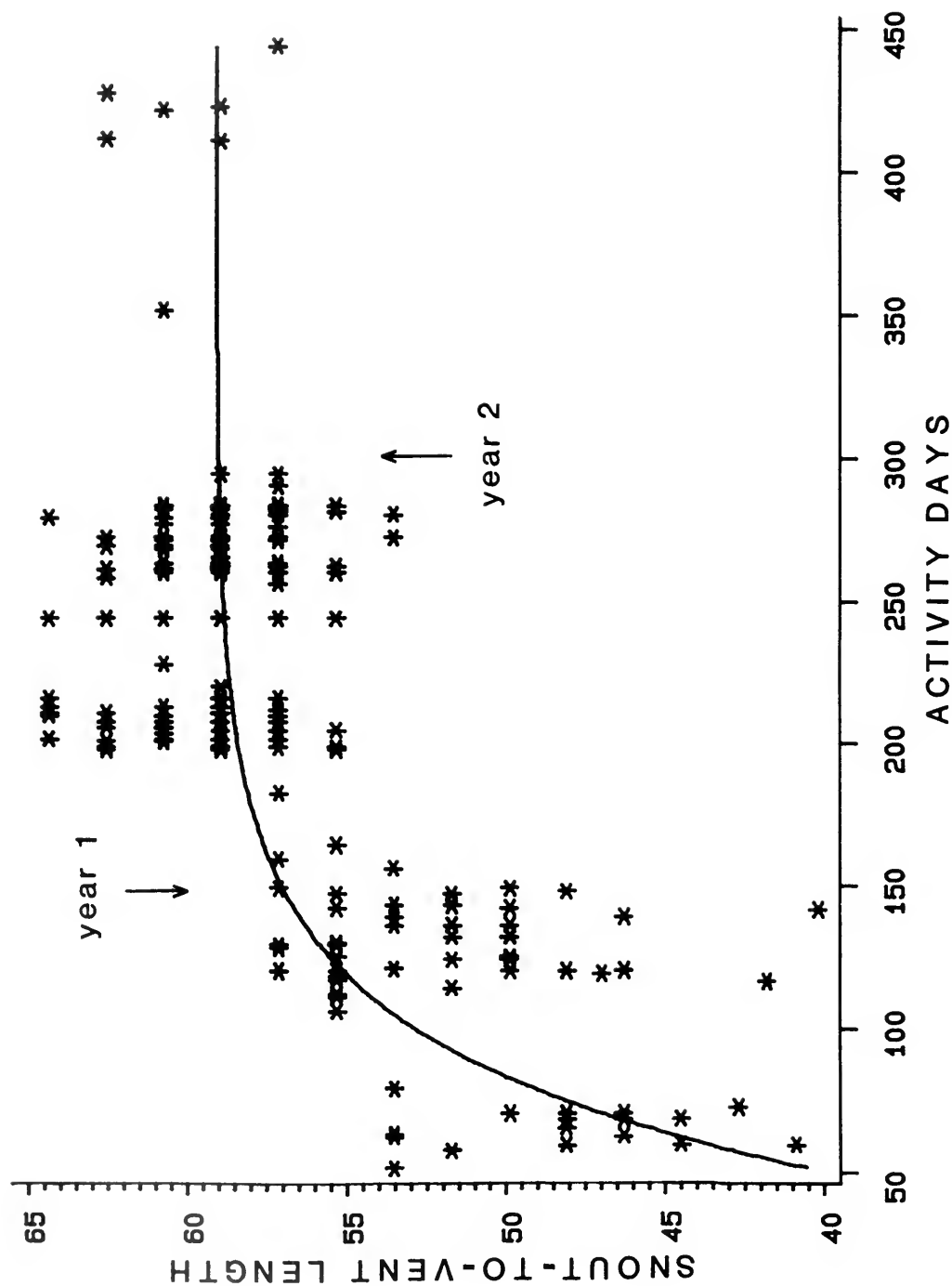


FIG. 4. Plot of snout-to-vent length for 229 toads of known age (transformed to activity days since metamorphosis, assuming 150 activity days per season), and Bertalanffy growth curve fitted to these data.

It is possible to determine a growth trajectory from recapture records of animals whose exact age and body size are known. Figure 4 shows snout-vent length plotted against activity days from 229 recapture events, combining male and female records. In order to account for the winter hibernation period during which time no activity or growth occurs (table 3), the age of each animal was adjusted by the number of activity days since metamorphosis. This was calculated by assuming that (1) all animals metamorphose on 1 July, and (2) activity in a season lasts from 1 May to the end of September, giving a total of five months or 150 activity days per season. These data reveal a period of rapid growth for the first two seasons, and that size increases to an asymptote at approximately 60 mm. A curve fitted to this growth data, determined by the nonlinear regression program of the Statistical Analysis System (1979), is also illustrated in Figure 4. The equation of the model used to determine snout-vent length is

$$B_0 \times (1.0 - e^{-B_1 \times \text{activity days}})$$

Fitting a Bertalanffy curve assumes that the observed data exhibit early, rapid growth approaching an asymptote and is appropriate for growth data such as those shown in Figure 4 (Kaufmann, 1981). The nonlinear estimate for B_0 , the asymptote, is 59.04 mm (0.32 SE), and for B_1 , the exponential damping parameter, 0.022 (0.001 SE).

The records of animals marked at metamorphosis, captured as juveniles or subadults, and subsequently recaptured as adults (whose sex could therefore be determined unambiguously) were examined for growth rate differences between the sexes. Table 4 shows male and female mean snout-vent lengths for four postmetamorphic age classes and for all adult records. Females are significantly larger than males ($P < 0.05$) at all age classes 14 months and older. The nonlinear growth curve estimated from these data showed that females grew faster (damping term smaller) during the period of rapid growth (B_1 males = 0.025, B_1 females = 0.018, $P < 0.05$), and that the female growth trajectory reached a higher asymptote (B_0 males = 57.89, B_0 females = 61.87, $P < 0.05$).

Sex Ratio at Breeding Sites and for Total Population

The observed sex ratio, defined as the ratio of the number of adult females captured to the total number of adults captured, is strongly biased to-

TABLE 4. Age-specific male and female mean snout-vent lengths (mm); females are significantly larger than males at all ages greater than 2 months.

Stage (age postmeta-morphosis)	Female mean (SE)	Male mean (SE)	t test
Juveniles (2 months)	48.1 (1.08) (N = 8)	48.0 (1.01) (N = 14)	$P > 0.5$
Subadults (11 months)	49.2 (0.99) (N = 9)	52.3 (0.72) (N = 31)	$P < 0.05$
Subadults (14 months)	60.9 (0.62) (N = 28)	58.2 (0.42) (N = 15)	*
Adults (23 months)	61.6 (0.67) (N = 14)	58.5 (0.25) (N = 52)	*
All adult records	62.2 (0.27) (N = 168)	58.8 (0.09) (N = 1025)	*

* Significance levels are not reported because many animals appear in several samples.

ward males within the spring breeding aggregations. For nights on which more than four toads were captured, in 1980 this ratio ranged from 0 to 0.6 (mean = 0.13), and in 1981 from 0 to 0.32 (mean = 0.10). During spring 1980 the most males caught at the breeding ponds in one night was 68, while the maximum number of females was only three.

This bias in the observed sex ratio could be explained by behavioral differences between the sexes causing males to be caught more often (e.g., males remaining in the ponds longer during the breeding season, and male advertisement calls), or by an actual male bias in the sex ratio of the adult population, perhaps caused by males maturing at an earlier age. However, records from animals captured in the summer and also during the breeding season show that the sex ratio in the adult population is actually not statistically different from 0.5. This subsample was used to estimate the adult sex ratio because (1) during the breeding season, it is possible to unambiguously determine the sex of each individual; and (2) the sex ratio in the summer capture records should not be biased by behavioral differences associated with reproduction. In this manner the population sex ratio was estimated as 0.46, which is not significantly different from 0.5.

Number of Adults per Breeding Aggregation and Total Population Size

The Lincoln-Petersen estimates (with 95% confidence intervals) of the male breeding population

size in each of the seven areas of the study site were 118 (71, 197); 118 (71, 197); 114 (73, 177); 35 (23, 54); 35 (23, 54); 162 (91, 286); and 360 (187, 692). The assumption that the entire adult male population is present in the ponds in the spring and that the adult sex ratio is 0.5 (see above) yields an estimate of 1,814 adult toads in the study area.

The second method for estimating population size per breeding area, a direct count of egg masses, gives a better indication of the reproductive potential of this population. This count for spring 1981 for each area was: 5, 13 (2), 29 (3), 8, 15 (5), 31 (2), and 56 (the numbers in parentheses are egg masses that did not produce larvae). This means that the total number of breeding females in the study area was 157, 150 of which successfully produced young.

Age-Specific Survivorship and Population Turnover Rate

The count of egg masses, electrophoretic introductions, individuals marked at metamorphosis, and mark-and-recapture records of individually marked toads can be used to estimate the number of individuals in all life history stages. Assuming a stable age distribution, the relative proportion of an initial cohort that survives to each age class can be used to estimate the survivorship probability to that age.

NUMBER OF EGGS—The count of 157 egg masses laid in 1981, combined with an estimate of 5,221 eggs/egg mass computed from Clarke's (1974) study of *Bufo woodhousei fowleri*, produces an estimate of 819,697 eggs deposited in 1981 in the West Beach study site. For the purposes of constructing a life table, I assume that the population size and the number of eggs deposited are approximately the same for all years.

NUMBER OF ONE-WEEK-OLD TADPOLES—Electrophoretically marked individuals were introduced into the pond one week after they were laid in the laboratory and can be used to estimate the size of this age class. In spring 1979, 17,089 electrophoretically marked tadpoles were introduced. Four of 152 subadults examined electrophoretically in 1980 were found to be electrophoretically marked. This yields a Lincoln-Petersen estimate for the total number of one-week-old tadpoles in the study site in 1979 of 649,382. Unfortunately, this estimate is very uncertain, with a 95% confidence interval of 179,229 to 1,916,976.

METAMORPHIC TOADLETS—A total of 6,079 toad-

lets were physically marked at metamorphosis during summer 1979. Of the 182 juveniles captured in fall 1979, 17 had been physically marked at metamorphosis. This yields an estimate of 65,081 (37,196–104,553) metamorphic toadlets in the population.

POSTMETAMORPHIC JUVENILES—Of the 95 subadults captured in spring 1980, 12 had been captured as juveniles in fall 1979. This yields an estimate of 1,440 (726–2,541) juveniles present in the population ($12/95 = 182/x$).

POPULATION TURNOVER AND NUMBER OF TWO-YEAR-OLD ADULTS—The turnover rate of the adult population is defined as the proportion of the adult breeding population that is composed of "new recruits," individuals that were prereproductive subadults during the preceding breeding season. Under the assumption of constant population size, 1.0 minus the turnover rate equals the adult survival rate. Individuals that were marked at metamorphosis in 1979 and entered the breeding population in 1981 can be used to estimate the turnover rate. The proportion of marked juveniles captured in fall 1979 was 0.093, and of marked subadults captured in spring 1980, 0.116. The average of these two estimates is 0.1045, suggesting that approximately 10% of the spring 1979 cohort was physically marked at metamorphosis. During spring 1981, out of 683 adults captured, 30 had been physically marked at metamorphosis in 1979. If 100% of the 1979 cohort had been marked at metamorphosis, I could expect to capture $30 \times (100\%/10.45\%) = 287$ animals in spring 1981 that had been marked at metamorphosis in spring 1979. This yields an estimate for the adult turnover rate of 0.42. (Projected number of new recruits captured/total number of adults captured = $287/683 = 0.42$.) The number of adults in the population, 1,814, estimated from the recaptures of males within the spring 1981 breeding season, times the turnover rate of 0.42, yields an estimate of a total of 762 new recruits into the breeding population each year.

SURVIVORSHIP SCHEDULE—These estimates of the number of individuals in the early life history stages, including two-year-old adults, are used to produce the life table illustrated in Figure 5. The natural logarithm of these estimates are plotted because a constant probability of survivorship is then indicated by a constant slope of the survivorship curve. The shape of this life table resembles a type III survivorship curve (Krebs, 1985), with lower survivorship at the early stages. The estimate of 762 new recruits into the two-year-old

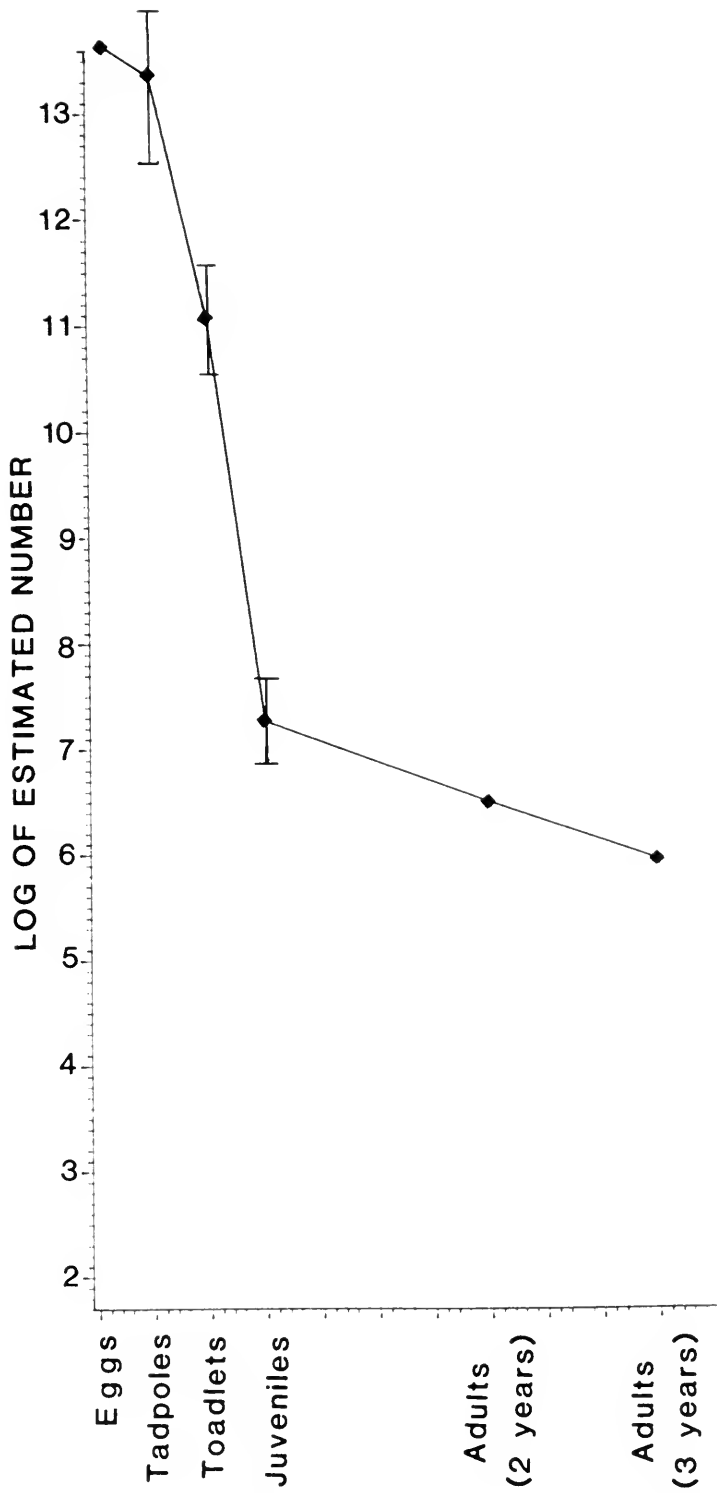


FIG. 5. Estimated population sizes (and 95% confidence intervals when appropriate) for all life history stages of Fowler's toad.

class was multiplied by 0.58 (1.0 minus the turnover rate) in order to estimate the number of three-year-old adults.

It is interesting to note that the independent estimate of the number of juveniles in the population lies on the same line as that produced by the projection of two- and three-year-old adults, determined by the adult turnover rate (fig. 5). This suggests that the per-year adult survivorship rate applies to all sizes beyond the 30-mm size class designated as juveniles. Dividing these population sizes by the number of eggs in the original cohort produces the following survivorship probabilities: one-week-old tadpoles, 0.792; metamorphic toadlets, 0.079; juveniles, 1.76×10^{-3} ; and two-year-old adults, 9.30×10^{-4} .

Discussion

Data on postmetamorphic growth can be used to evaluate one of the methods of determining the demographic parameters of amphibian populations. Turner (1960) suggested dividing a study population into age classes depending on size, determining yearly growth rates and maximum size in the population, and then calculating maximum life span as the number of years required to grow to the observed maximum size. This would not work very well in this population of Fowler's toads, given that many individuals reach what seems to be the maximum size in the population by their second year of growth (fig. 4). The distribution of sizes in the spring and fall records (fig. 3) do suggest that one could accurately separate this population into two age classes: (1) adults and (2) all juveniles and subadults less than two years old. In this manner, the age of a large number of animals with a high chance of survivorship could be determined without having to mark them at the time of metamorphosis. These could then be further studied in order to determine the demographic characteristics of the population. However, differentiation between ages greater than the age of first reproduction may not be generally possible using this technique.

The shape of the survivorship curve (fig. 5) raises some interesting questions concerning the antipredator defenses of young toads. It has been suggested that toads are distasteful at all life history stages (eggs, Licht, 1968; tadpoles, Voris & Bacon, 1966; metamorphic toadlets, Brodie et al., 1978; and many studies report the toxicity of the adults, e.g., Licht & Low, 1968). However, in Fig-

ure 5, survivorship from metamorphosis to the juvenile stage is as low as the survivorship of the tadpoles. The survivorship curve shows a significant increase in survivorship only at the juvenile stage, when it becomes as high as the adult survivorship. Licht (1967) showed that glandular parotids did not develop until three to four weeks after metamorphosis in three species of toads, and examination of metamorphic toadlets and toadlets from the first postmetamorphic month in the West Beach study site showed that there was no raised gland in the region that would eventually develop into the parotids. This suggests that the increased survivorship associated with effective antipredator chemicals may not develop in this species until after the juvenile period.

One of the most important parameters determining population growth rate is the age at first reproduction (Ricklefs, 1979). In this study individuals bred for the first time two years after metamorphosis. This estimate agrees with Clarke's (1974) study of postmetamorphic growth in Fowler's toad. In a review of postmetamorphic growth in anurans, Turner (1960) lists the following years to sexual maturity for *Bufo* species: *Bufo terrestris* males 2, females 2; *B. valliceps* males 1, females 1?; and *B. quercicus* males 1, females 2. Zug and Zug (1979) estimated that *B. marinus* reached the size of sexual maturity one year after metamorphosis, although all animals might not breed that early. Thus Fowler's toads in this part of their range mature at the average time for the genus *Bufo*.

The probability of movement between areas was highest from metamorphosis to the juvenile stage (48%) compared to the older age classes (12%–17%; fig. 2, table 2). This pattern of high dispersal during the juvenile or subadult stage, followed by more restricted home ranges for adults, is common among vertebrate species. Wilson (1975) gives several examples of this pattern and suggests that it might be explained by these ages having the highest reproductive value.

Several demographic characteristics of this population suggest that the probability of local extinction is not very high. During the period of this study, large numbers of metamorphic toadlets were produced from all areas of the park. The adult population was estimated as approximately 1,800 individuals. Although only about 150 females produced egg masses in one year, these masses would be expected to yield at least 750,000 eggs. If the estimate of survivorship to the two-year age class is accurate (0.1%), then 750 "new recruits" would join the reproductive ranks each year. The esti-

mate of adult population size between 1,000 and 2,000 seems reasonable, given this number of new recruits and an adult survival rate of 0.58. The electrophoretic survey suggested that this insular population in the West Beach Unit is relatively homozygous compared to other populations of Fowler's toads. However, given the estimated size and possible constancy of this population, it is not likely that this high level of homozygosity has been caused by a genetic "bottleneck" effect associated with small population size (Crow & Kimura, 1970).

Given the history of local extinction in this species, the continual habitat destruction, and the intense human use of this area, it is important to determine the recolonization potential of this species based on the observed pattern of dispersal. This potential is difficult to estimate because migration could only be observed among the seven subdivisions of the study site. However, the shape of the dispersal curve from metamorphosis to the adult stage did show a rapid decrease in the probability of dispersal as the distance from the natal area increased above two or three steps (fig. 2C). This implies that the potential for long-range dispersal is very limited in this species. Given that the breeding areas of this species are restricted by specific habitat requirements and intense utilization of the dunes by humans, local extinctions of Fowler's toads could be expected to be permanent events.

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